SECONDARY PRODUCTIVITY OF TERRESTRIAL ECOSYSTEMS
ED. K. PETRUSEWICZ

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Mercury S. GHILAROV

Laboratory of Soil Zoology,
Institute of Animal Morphology,
Academy of Sciences USSR,
Moscow, USSR

3.2.6. Abundance, biomass and vertical distribution of soil animals in different zones

In the majority of climatic zones the biomass of soil animals comprises the principal part of secondary production.

Only in dark, tropical rain-forests is the soil stratum poor in animals, because representatives of the soil fauna in other zones here become suprasoil dwellers.

There are numerous data showing that the weight of earthworms and other large invertebrates in pasture soil is greater than the weight of cattle grazing upon it, that one quarter of the plant matter eaten by cows is afterwards consumed by dung-beetles, and so on.

Such picturesque comparisons show that the biomass of soil fauna is really very great. In terms of IBP problems dealing with ways to heighten the prosperity of mankind by increasing the production of organic matter consumed by man, it is necessary to stress that productivity of soil animals is of no immediate importance for humanity. Man usually does not consume soil animals, and the significance of soil animals even in the nutrition of poultry is rather modest. But the indirect significance of soil dwellers for the man is extremely high, though often it is underestimated or even neglected.

Soil animals are a potent, positive factor in soil formation and soil fertility, and as the latter is of fundamental importance to primary productivity, the study of soil animals — of their abundance, biomass and character of activitity — is closely connected to the problems of the primary production.

Many representatives of phytophagous soil invertebrates, chiefly insects, nematodes and some mites, are very noxious destroyers of living plants.

Their activity affects primary production, causing enormous loss in yields of crop of cultivated or edible plants.

In the present communication the reporter will try to elucidate some principal regularities of the distribution of soil invertebrates in different climatic zones, to show the connection between abundance and biomass of soil animals and the character of the soil.

The soil — influencing activity of any community of soil animals depends not only on the general biomass and climatic conditions, but also on physiological, morphological and ecological properties of different animal categories, species and individuals.

To date it has been possible only to trace some regularities in the zonal distribution of non-microscopic animals, principally those which are easily detected by soil fauna sampling when using hand sifting. These groups of soil animals, chiefly arthropods and earthworms, have been the subject of my investigations in different zones from the tundra to subtropics; I have investigated zonal and azonal types of soil in various natural communities and in arable lands.

For the general purposes of the IBP it is especially interesting to evaluate the zoological activity in different undisturbed soils of various climatic zones. Accurate data on the biomass of soil animals in different conditions are rather scarce; probably nowhere has there been simultaneous evaluation of the numbers and weight of all the soil animal groups. I should like to mention as being rather accurate the data for Belgian forests, by Nef (1957); he found circa 1000 kg per ha in mull soil, in forests with sweet humus, but less than 300 kg per ha in raw, rough humus. But quantitative differences are not as great as qualitative ones are: in sweet humus soil about 70% of biomass is that of earthworms, 10% of nematodes, 20% of arthropods: whereas in row-humus soil 30% of the animal biomass consist of enchytraeids, 50% of arthropods, and 20% of nematodes. Probably the highest figures are to be found in counts made by Stöckli (1957). According to him the biomass of mountain meadow soil invertebrates in Switzerland is approximately as follows (per sq. m): earthworms — 400 g, larger arthropods and molluscs — 80 g, protozoans — 37 g, nematodes — 5 g, enchytraeids — 2 g, microarthropods — 2 g. Probably microarthropods and nematodes are underestimated. The total comprises 536 g per sq. m, or more than 5 metric tons per 1 ha. But in olains in Hungary, meadow soil contains not 400 g of lumbricids, but only 135 g per sq. m (correspondingly 1350 kg per 1 ha), whereas in arable soil only 18 g of these invertebrates is to be found per 1 sq. m (180 kg/ha).

These examples show the great variability in the biomass of animals even within the same zone under similar types of vegetation and the still greater variations under different plant covers. But it is necessary to stress that the total weight of living organisms belonging to different groups is not comparable: e.g. although the water content in earthworms is much higher than that in beetles, it is not water, but rather active plasma, which determines the activity of an organism. Dry weight also does not allow valid comparisons — many insects and snails contain to much inert dry matter (carapace, shell, etc.). Dry weight is as doubtful an index as is living weight. Therefore, there have been made attempts to establish the significance of different animal groups in the soil according to their physiological activity, measured as the "metabolic rate" according to the consumption of O_2 or removing of CO_2.

Very nice, precise experiments by Nielsen (1960) have shown that the respiration rate of nematodes is 10 times higher than that of segmented worms, earthworms including.

Thus, it seems that in the turnover of organic matter, the smaller animals are of greater importance than bigger ones. Even within the same group of soil invertebrates, for instance earthworms, such a regularity may be observed. As an illustration, the data of Byzova (1965) (Fig. 1) on the uptake of O_2 by earthworms of various size, belonging to different species and even to the same species, may be used.

There are numerous data showing similar regularities. There has been proposed by Charles Elton the term "pyramid of numbers"; as a rule the number of predators is less than that of prey, while the size of predators is bigger than that of prey. Thus the larger the animals in any food chain the less is their abundance. The "pyramid of numbers" was stated also by Williams (1942) with respect to the soil animals in Panamanian tropical rain forest.

Regularities of this kind seem to be more complete. It was shown in my early publication (Ghilarov 1943), that the predator—prey systems are not the only cause of such regularities. Probably the main cause is that in such a heterogeneous environment as the soil, the possibility of finding all the conditions necessary for the existence and activity of any organisms is greater, the smaller the size of the organism. Young individuals of any given species are always smaller and more numerous than the adults are (the mortality being higher in early stages). The duration of development is, as a rule, longer in bigger animals than in smaller ones, and consequently the probability of reaching adulthood and leaving progeny is greater in smaller animals than bigger ones. It is worthwhile to add that in pyramids of numbers, in addition to the general rule that larger animals need a greater amount of food, there is also a definite relation between the size of the food units consumed and the size of the feeding organism, if the types of feeding are similar.

Generally "vital space", the so called "range of an individual", is wider in bigger animals than in smaller ones. Therefore, the biomass of soil animals belonging to different dimensional groups is of about the same order. The production of the total number of organisms of a given linear size category, when involuted to the third degree, is of a magnitude of similar order within soil of any given type (Fig. 2). This relationship must be due to the fact that soil animals of different size occupy different media within the same soil.

The smallest animals, such as soil protozoans, rotifers, small nematodes, etc., inhabit not the soil as a whole, but only films of water around and between solid particles and aggregates. For larger, but still small inhabitants, such as microarthropods, mites, and colembola, the soil as an environment may be considered as a system of relatively large caves. The cavities, tunnels, etc., are often larger than body size, and microarthropods move in the soil as if they were on the walls of caves. Only the larger invertebrates (earthworms, insect larvae, myriapods, etc.) inhabit the soil as a whole.

The soil complex of biocenoses is subdivided into separate categories, characterized by the dimensions of animals entering the soil stratum of the biocenoses. The smaller representatives of soil animals, although of higher activity with respect to consumption of organic matter, cannot perform such work as is performed by larger ones; soil nematodes, although of the same total biomass as earthworms, never can perform such changes in the soil as are done by *Allobophora caliginosa* Sav. in fields and meadows or *Lumbricus terrestris* L. in forest soils.

The criteria of biomass or energy flow are unsuitable for estimating the soil forming activity of soil animals. In natural conditions the effect on the earth surface, on soil formation, by the whole biocenose is much higher than simply the sum of actions of its members if measured separately. Thus animals are influencing the litter destruction, not separately, but together in an interaction with microorganisms. The destruction of litter proceeds in the presence of soil animals twice as fast and more fully than in the absence of animals (when they are repelled by means of naphthalene) as it has been proved in the experiments carried out by Kurcheva (1960, 1964), who applied the method developed by the author of this report. The addition of soil invertebrates proves this, too (Tab. I, II). Even the isolation of the leaves from larger animals, as has been proved in many experiments by Edwards and Heath (1964) and other investigators, who experimentally isolated decomposing organic matter from larger invertebrates by means of nylon net bags (Fig. 3). Without bigger animals the decomposition performed by microorganisms (and smaller animals as well) proceeds much slower than in presence of earthworms and other bigger animals. The same is to be observed when studying the decomposition rate of timber in natural conditions, as proved by the averaged data of Mamaev (Fig. 4).

Of special importance is the deep chanelling of the soil performed by larger invertebrates, the increase of soil porosity and respectively aeration and drainage of the soil, the formation of stable granular structure of the soil, etc.

To evaluate the significance of the soil animals in primary production (that is, the very problem concerning soil organisms) it is necessary to know what they really do in the soil! To begin with it is necessary to obtain data on the nutrition of different groups. The ratio between predators and animals feeding in other ways is of a more or less constant value: among representatives of mesofauna (Ghilarov 1941), predators compose usually ca 10% 7—20%). But it is often very difficult to classify animals according to the mode of their nutrition. It depends often on environmental conditions. Ground beetle larvae (*Pterostichus*) can be either carnivorous or plant eaters. Chafer larvae of the same species may be saprophagous or phytophagous (Ghilarov 1937).

In moist soils which are rich in humus, the bulk of biomass consists of saprophagous species, whereas in dry soil which is poor in humus, the bulk consists of phytophagous ones; soil inhabiting pests are more abundant and noxious in arid than humid zones.

Up to date no accurate data have been reported on the whole soil stratum of the biocenose in any locality. It is necessary to obtain such data as soon as possible for different zones, and to evaluate the number, biomass and activity of all groups of soil animals in relation to their effect on primary production.

All the characters of the soil depend on the activity of soil inhabiting animals, and reciprocally, soil dwellers depend on soil conditions. Therefore, there are close correlations between the soil fauna and properties of the soil. One of the characters most significant with respect to the fertility of the soil is the amount, type and vertical distribution of humus — this character is also of primary value for the natural classification of soils. The depth of the humus horizon depends on the composition of soil fauna and on the ecological properties of soil invertebrates, their vertical migration in particular.

Because I have studied in different zones only the larger invertebrates, my data, especially numeric ones, will be restricted principally to this dimensional group of animals, such as earthworms and insect larvae.

It is not only subterranean parts of plants which serve as the source of humus formation in the soil, but also fallen leaves and other supraterranean parts of the plants, which are buried into the soil due to the activity of soil invertebrates. Kostychev (1886) claimed that fallen leaves and other supraterranean parts of the plants can not serve as a source of humus because insoluble organic substances do not penetrate deeply, being filtered by the soil. However, the penetration of plant residues from the soil surface deep into the soil is achieved simply by the digging activity of invertebrates, which create by their vertical migrations in the soil the non-capillary porosity, thus also permitting the drawing in of fragmented plant remains by water precipitation. Apart from this, the conditions in the intestine of invertebrates are favourable for humification, which starts here and continues in the excrements, with which the invertebrates bring a large amount of organic matter into the depth of the soil.

An investigation of the interrelation between the vertical distribution of humus, root systems and soil invertebrates in the soil made it possible to reveal certain correlations (Fig. 5). The soil layers rich in humus, consisting of granular, structural particles and penetrated with passage-ways, are richest in both plant roots and invertebrates. The main mass of the roots is concentrated in the A_1 horizon; the animals are abundantly represented here. It is mainly in this horizon that fallen leaves and other supraterranean parts of plants are buried in the soil; here their decomposition and humification occur, and animals play important role in these processes.

The lower border of the humus horizon coincides with the lower border of the distribution of the main mass of plant root systems, with the penetration into the soil of the bulk of soil invertebrates, and with the lower border of the well aerated layer. These borders are mutually connected and interdependent. The accumulation of humus in a given soil layer is related to the development in it of plant root systems, to the incorporation of fallen leaves and other supraterranean parts of plants into it due to the animals, and to the decay of these materials which also results the participation of the animals.

The distribution of the root system is related to the thickness of the humus layer, the plants utilizing the salts released in the course of mineralization of organic remains. The penetration of the roots into the depth is facilitated by the digging activity of animals (Wyssotsky 1900, Jacot 1936). The border lines limiting vertical distribution of the soil animals are determinated, in turn, by the depth of root penetration (for phytophagous species) and by the thickness of the humus layer (for saprophagous ones). Thus, all the links of the dynamic soil complex — plant root systems, invertebrates and soil humus — are interrelated (Ghilarov 1947).

In more humid regions, when the soil is saturated with moisture the activity of soil dwelling animals and aerobic microorganisms is impossible in deep horizons due to oxygen deficiency. During such periods all the processes of decomposition and mineralization of fallen leaves, and of other supraterranean parts of plants, occur mainly at the soil surface and in the litter where all the soil dwelling invertebrates concentrate. With the drying up of soil and the concomitant improvement in its aeration, the processes of destruction of the organic matter by soil invertebrates (especially by such ones as earthworms, *Lamellicornia* larvae, etc.) transport organic matter deep into the soil where the products of mineralization of plant remains are utilized by the more deeply penetrating roots. Therefore, the lower border of the main mass of the roots coincides with that of the aerated soil layer.

An increase in the population density of soil invertebrates, which are the main agents of increase in the non-capillary porosity of soil of a given texture, contributes also to the deepening of the humus horizon. Therefore, correlations between the character of the soil profile and the abundance (Fig. 7 below) and composition of the population of soil invertebrates are very distinct. This can be illustrated by data on a comparison of the soil invertebrate communities in different zonal soil types under zonal vegetation types.

In the moss-lichen and even in the moss-shrub tundra, the accumulative soil horizon is undeveloped because plant remains which are constantly saturated with moisture are unfavourable for the development of animals. That is why the animal groups characteristic of the soil in other zones are concentrated here in the moss soil (Fig. 6). To such animals belong: springtails, *Onychiurus armatus* Tullb.; enchytraeids; earthworms, *Eisenia nordenskioldi* Eis.; the larvae of *Sericus brunneus* L.; *Byrrhidae, Tipulidae* and others (Stebaev 1952). A small biomass of soil animals (up to 17—30 g/sq. m), and the impossibility of migrations downwards due to the excessive moisture and low temperatures, explain the fact that invertebrates do not bury plant remains into the depth of the soil. It also explains the fact that the accumulative horizon (A_1) is not expressed, the plant remains being accumulated on the surface (A_0). In the shrub tundra litter-dwelling species of invertebrates (e.g. *Dendrobaena octaedra* Sav.) appear under the dwarf birch shrubs, but the thickness of the accumulative horizon (A_1) does not exceed 1 cm even in gley-podzol soils of such dwarf birch vegetation (Fig. 7).

In podzol-gley soils the composition of population of soil dwellers is more diverse than in the tundra; the population density, however, is low and soil inhabitants are restricted to the surface layer, mainly to the litter. Under the zonal types of *Piceetum*, click-beetle larvea, *Corymbites cyneus* L., *Orithales serraticorrnis* Payk., *Eanus costalis* Payk., *Athous subfuscus* Müll., many hygrophilous and even semi-aquatic dipterous larvae (*Tendipedidae, Limoniidae, Tipulidae*) occur and are the principal destroyers of fallen leaves and others supraterranean parts of the plants; among the earthworms the surface litter dwelling hygrophilous species, *Dendrobaena octaedra* Sav., occurs here.

Due to the high moisture of the ground here, the inhabitants are represented by the forms which are active only at the surface; consequently the humus horizon is not developed. The fallen leaves and other supraterranean parts of the plants are not incorporated into the soil by the animals; only soluble products of their decay penetrate the soil thus determining the development of the podzolic horizon, A_2. Correspondingly, the root systems of even such a taiga edificator as the firtree are located superficially (Fig. 8).

In souther portions of the podzole zone there is an increase in the population density of soil invertebrates and the diversity of their faunal composition; a greater warming by the sun and drying of the soil allow the animals to migrate deeper into the soil. Among the click-beetle larvae *Athous subfuscus* Müll. is prevailing, the population density and the number of the earthworms species increase, and *Biastus tenuis* Eis. occurs along with the litter species, *D. octaedra* Sav. In the sites where the soil is underlaid by calciferous rocks on the other hand *Octolasium lacetum* Orley occurs. Dipterous larvae, *Tipulidae* and *Bibionidae*, are also encountered, being represented by less hygrophilous groups than in the north. Of the diplopods (which are not important litter destroyers in the taiga) only *Polyzonium germanicum* L. is common; its population density is low. Of centipedes only litter dwelling lithobiids are distributed in the forests on the podzol. As a result of the activity of soil dwelling invertebrates which are able to migrate vertically to the south of the taiga the layer into which the fallen leaves and other supraterranean parts of the plants are incorporated is somewhat deeper, even under the *Piceetum*. This leads to the formation of an accumulative horizon (A_1) intrinsic to the dern-podzol soils.

In the zone of mixed forests, where the soils are dern and feebly podzolized (Fig. 9), the role of earthworms among large-sized soil dwelling invertebrates increases. Of the earthworms, along with the litter species *D. octaedra* Sav., *Allobophora caliginosa* Sav., becomes very important, as do species of the genus *Lumbricus*, such as *L. rubellus* Hoffm. and *L. terrestris* L. (which makes deep holes and passage-ways but which is feeding on the litter). Among click-beetle larvae, both *Athous subfuscus* and *Dalopius marginatus* L. prevail in the litter. Such carabid species as *Calathus micropterus* L. and other intrinsic for the taiga zone occur in the zone of mixed forest, too.

In the north of the taiga zone the only diplopod which occurs is *Polyzonium germanicum* L., while *Juloidea* and *Polydesmus complanatus* L. are also common in mixed forest (Perel 1962). Because of the combined activity of various components of soil fauna, the A_1 horizon attains a thickness of 10—15 cm in feebly podzolized dern soils, whereas multiple humus leakages are found in the podzolic horizon A_2.

In grey forest soils (Fig. 10), e.g. under oak forests with linden, it is not litter earthworms but the true soil dwelling ones, *Allobophora caliginosa* Sav. and *Eisenia rosea* Sav., which acquire leading significance. Among soil dwelling click-beetle larvae, *Dolopius marginatus* L. is common; *Athous haemorrhoidalis* F. is common in forests with the strongly developed dern cover formation, and *Selatosomus aeneus* L. is common in lighter (sandy loam) soils. Among the dipterous larvae *Brachycera* are prevailing, instead of the *Nematocera* which predominate in more northern soils. The appearance of white-grubs, particularly *Melolontha hippocastani* F. and *Phyllopertha horticola* L., is very significant. The main components of soil fauna undertake vertical migrations. The *Juloidea* complex becomes more diverse, while in the *Chilopoda* complex there appear not only litter dwelling *Lithobiidae*, but burrowing *Geophilidae* as well. Correspondingly, the A_1 horizon is thicker in grey forest soils when compared to that in dern-podzolic ones (up to 30—40 cm).

In the chernozems (black soils) of the forest-steppe zone and in the steppe in particular, the principle of the "change of strata" (Ghilarov 1951) is distinctly pronounced. This principle may be expressed as follows: many forms dwelling at or above the soil surface in more humid zones are part of the life in the soil horizon in arid zones. In the chernozem steppes deep dwelling *Eisenia rosea* are common among the earthworms, and the white grub community is very numerous and diverse (species of the genera *Anispolia*, *Rhizotrogus* and others); of the click-beetles *Selatosomus latus* F., *Agriotes sputator* L. and *A. gurgistanus* Fald. are most numerous (in the north the representatives of the genus *Agriotes* in open habitats); soil dwelling tenebrionid and alleculid-larvae appear in mass numbers (in deciduous forests other species of these families develop in the decaying wood). Soil dwelling longicorn larvae (*Dorcadion* spp.), leaf-beet larvae (*Eumoplinae*) and many other forms appear also.

Hygrophilous and litter dwelling forms disappear from the dipterous insects and are replaced by typically soil dwelling ones (*Therevidae, Asilidae* and others); the significance of the dipterous larvae decreases in comparison to the forest zones. The ants which inhabit drier habitats, such as tussocks, etc., in the taiga zone build deep subterranean nests in the steppe (*Lasius alienus* Först. and others). Geophilids are prevailing among chilopods, *Cryptopidae* appear, etc.

A periodical change in the strata of activity of the soil dwelling invertebrates is observed in the chernozems. In spring soil inhabitants are active at the surface, where fallen leaves and other supraterranean parts of the plants become buried in the soil. With the onset of the dry weather the horizons of activity of soil animals are more downward. Against the back-ground of the gradual migration of the invertebrates into the depth of the soil (saprovores migrate deeper, while herbivores remain at the surface where they restore their supply of moisture at the expense of soft plant roots), intermittent migrations of the animals to the surface are observed; these movements have both a diurnal rhythm (depending upon the temperature and moisture of the air at the soil surface) and are related to weather conditions (lifts follow rainfalls). An active mixing of mineral soil particles with plant remains is accomplished by the invertebrates at different periods and at different depths, which contributes to the formation of the granular structure of the soil.

Corresponding to the continuous deep migration of the invertebrates, the humus penetrates to a considerable depth too. At many sites thick chernozems have the humus horizon down to 100—200 cm; in this case saprovores (e.g. earthworms, colembols, etc.), herbivores (e.g. weevil larvae) and predatory geophilids migrate down to the same depth (Arnoldi, Ghilarov 1964) (Fig. 11, 12).

In semi-desert chestnut the total population density of the invertebrates, particularly of hygrophilous forms, decreases. The earthworms, the larvae of nematocerous *Diptera,* and many other active agents of soil formation practically disappear. The distribution of the active invertebrates in deeper horizons is often limited by the insalination.

In grey desert soils (sierozems) the short period of invertebrate activity at the soil surface is replaced by their downward migration, often to considerable depth (e.g. the larvae of *Pleonomus tereticollis* Men. and *Prinous turkestanicus* Sem. migrate down to 2 m, and the termites, *Hodotermitidae,* migrate much deeper). The mass of fallen leaves and other supraterranean parts of the plants is insignificant in the desert; correspondingly, the humus content of soil is low in grey desert soils, but its content gradually changes with the depth (Fig. 13).

In the desert the soil forming activity of animals is clearly manifest, since in most cases it is a small number of species which are acting as soil forming agents, and their action upon the soil is quite distinct (woodlice of the genus *Hemilepistus* in clay-plots, the termites, *Anacanthotermes ahngerianus* Jacobs. on sandy loams, and others). Therefore, the attention of soil scientists (Neustruev 1913, Dimo 1955) was attracted to the soil forming activity of the animals just in the deserts, although both the population density and the role of the animals in the soil formation in deserts is less significant than in other zones.

The fauna of the solonchaks (salinated soils) in arid zones, where the existence of most soil dwelling invertebrates is impossible due to high salinity, is very unique. The washing of excessive salts from upper horizons of insalinated soils leads to a gradual increase in the accumulative horizon, the lower border of which is determined by the depth to which invertebrates can penetrate in dry seasons without contacting soil solution containing a high amount of salts. On the solonchaks — solonets complex soil plots — the insect larvae connected with plant roots (*Curculionidae, Eumolpinae*) are very common components of the soil fauna, although representatives of typical soil dwelling groups (*Tenebrionidae, Elateridae, Carabidae* and others) do occur as well.

The relation of the development and character of the humus horizon, and of the entire soil profile, with the invertebrate community can easily be understood. Digging their tunnels, clearing root debris, and developing the soil structure, the invertebrates contribute to the deeping of the soil horizon. Even in soils with a thick humus horizon, e.g. in dark brown soils of the walnut and apple-tree forests of the Fergana mountains, or in the chernozems near Kursk, the penetration of soil dwelling animals (earthworms, onychiurids) into the loess and into the C horizon is observed (Ghilarov 1953, 1960). At the sites of such penetration, dark coloured organic material is incorporated into loess, humus leakages are formed, and the soil profile deepens.

In humid subtropics of the zone of red and yellow soils, the character of the humus horizon is very like that of podzolic soils, and generally these soils are in many respects similar to podzolic. This is related to the high degree of humidity of the soil, which allows invertebrates to inhabit only the superficial layer of the soil.

It is of interest that in tropical rain forests (Fig. 14), where the air under the tree canopy is always saturated with water vapour, representatives of animal groups which in other zone are associated with the soil stratum, can dwell on the suprasoil parts of trees and shrubs. Therefore, no true profile is formed in tropical forests, and the fertility of tropical soils is surprisingly low. Cultivated deforestated areas in the tropics are exhausted within one decade without fertilization. The luxurious tropical vegetation depends not on the amount of nutrients in the soil, but on the rate of matter turnover and animals are one of the links in this turnover.

In tropical forests something similar to the formation of soil occurs on twigs (Fig. 15), where a stratification of "suspended soil" is rather well expressed.

It is possible now to make some general conclusions concerning the biomass of soil animals in different zones.

The most abundant populations are in grey forest and in chernozem soils; in the latter the animals are also the more evenly distributed throughout the soil profile.

The data concerning biomass are rather scarce and have been obtained with different degrees of accuracy for the different soils. These data are shown in Tab. III. Certainly the same regularity that was obtained when studying numbers of a certain dimensional group, are reflected in data on biomass regularity.

In summary, it may be concluded that the secondary productivity of soil invertebrates depends on zonal climatic and vegetation conditions, that the greater the secondary production and activity of the soil stratum biocenose, the greater is its influence on the soil itself and on primary productivity.

Although the secondary production of the soil stratum of any communities is of no immediate practical importance, its indirect significance is very high and must be studied in the framework of the IBP.

The elaboration of methods to increase the abundance and activity of soil forming animals must be a primary practical problem of soil zoology.

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Table I

Acceleration of oak dead leaf destruction in natural conditions and under the influence of added invertebrates and additional wetting of plots (field experiments in National Park near of Kursk; counts by Kurcheva)

Variant of experiment	Amount of decomposed oak leaves (dry weight) g/1 sq. m
Check plots	73 ± 2
Invertebrates added only	101 ± 4
Plots periodically wetted without added animals	116 ± 2
The same wetting plus the adding of animals	158 ± 2

Table II

The population density of larger invertebrates in litter and top soil of the oak wood, and the number of invertebrates added in experiments mentioned in Table I (National Park near Kursk; estimations by Kurcheva)

Name of invertebrate	Mean number per 1 sq. m before the experiment per 1 sq. m (check)	Number of animals added per 1 sq. m in the experiment
Lumbricidae	146	172
Enchytraeidae	710	700
Diplopoda	18	50
Isopoda	5	50

Table III

The average biomass (kg/ha) of soil animals in different zones under the natural undisturbed vegetation (calculated by Chernov, with author's corrections)

Zone	Biomass kg/ha
Tundra (moss tundra)	30
Taiga (coniferous forest)	200
Broadleaved deciduous forest	1000
Steppes	250
Semidesert	10

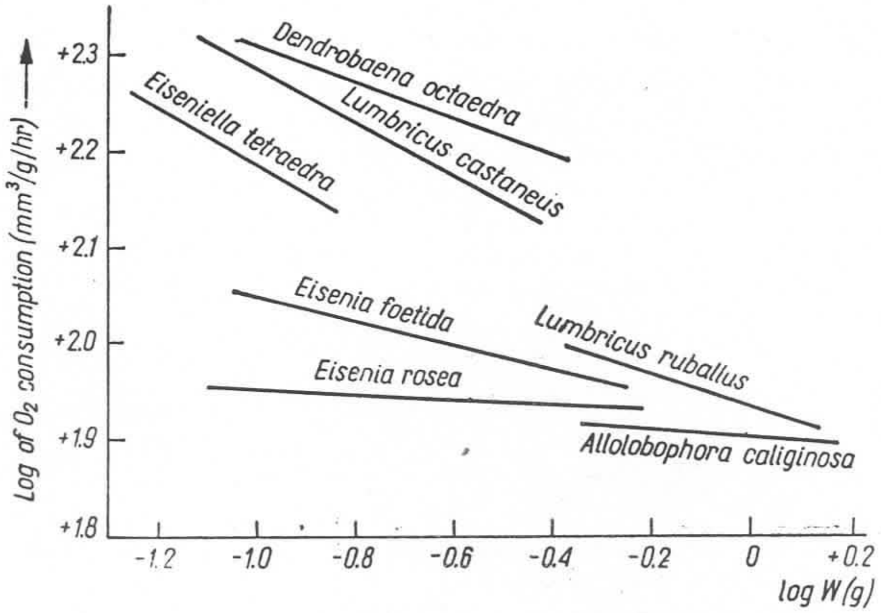


Fig. 1. Oxygen uptake by earthworms of different size (of the same species and of different species)

Double logarithmic scale, abscissa — weight of the animal, ordinate — oxygen uptake

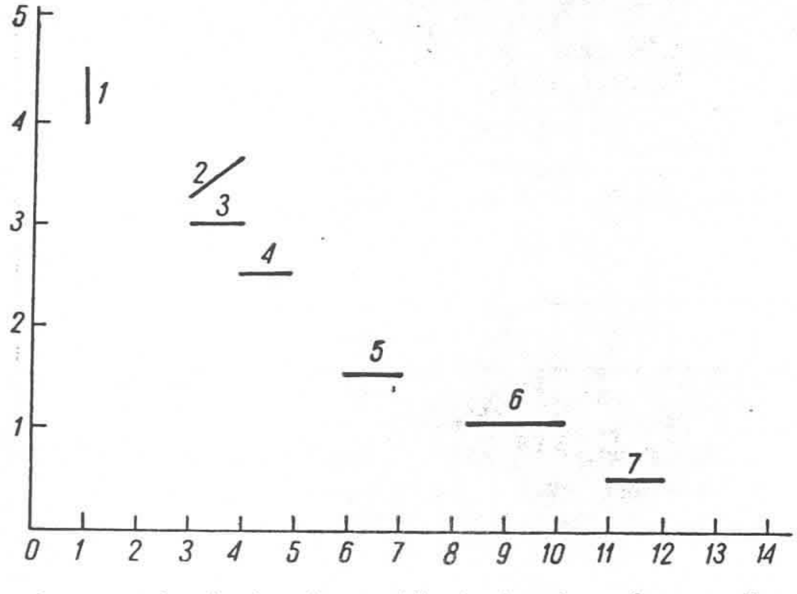


Fig. 2. Correlation between the size in microns (abscissa) and numbers per 1 sq. m (ordinate) or different dimensional groups of animals (double logarithmic scale)

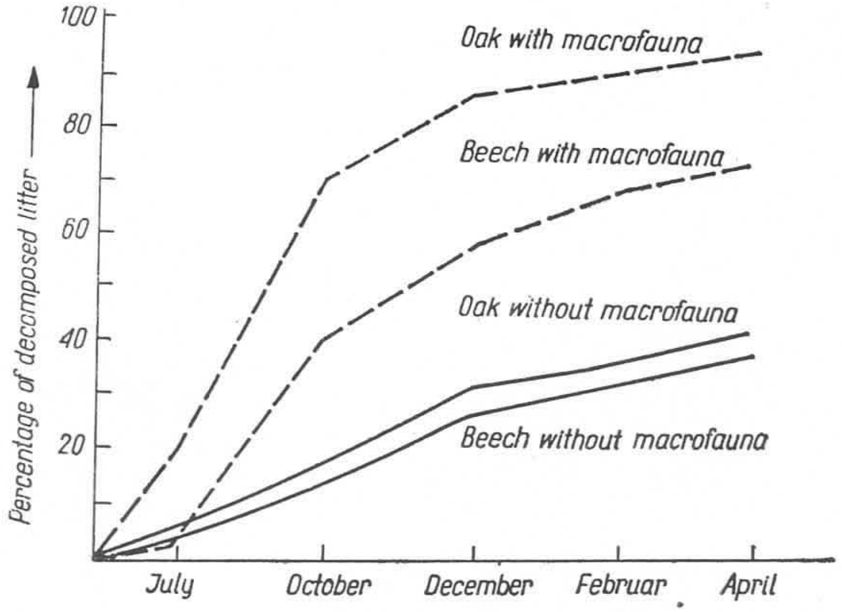


Fig. 3. Rate of oak and beech litter destruction without pariitcpation of larger invertebrates and under the influence of action of larger invertebrates (according to the data by Edwards and Heath)

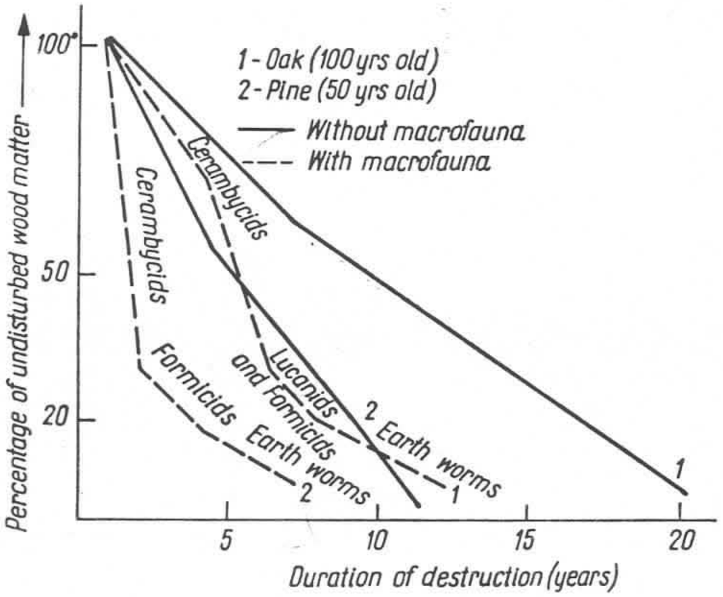


Fig. 4. The rate of wood timber destruction in natural conditions without the influence of saprovore animals and with their participation (brown fungus decay of oak wood and blue fungus of pin oicaoa e,tycdnɹo wcgd doə data by Mamaev)

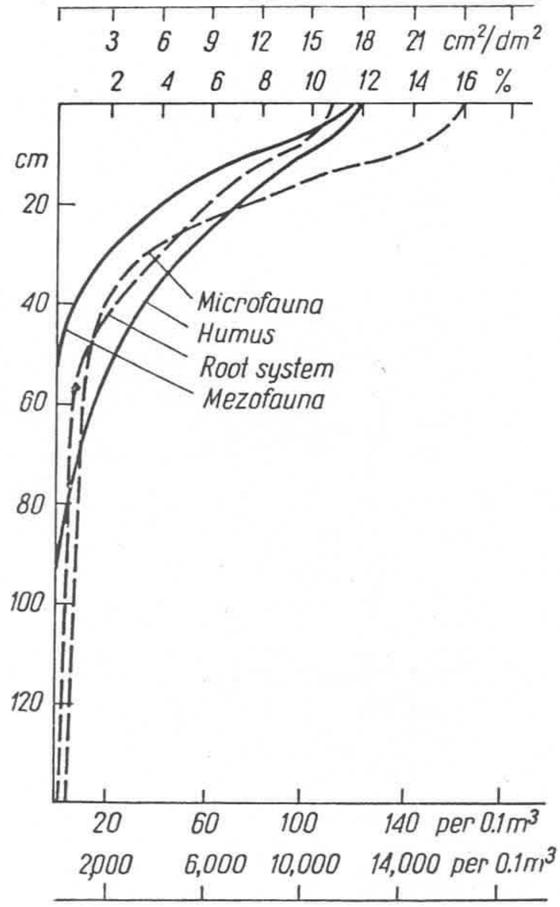


Fig. 5. The average annual distribution of larger soil invertebrates, of microarthropods, of humus, and of roots in brown soil in Fergana Mountain forests (according to Ghilarov 1947)

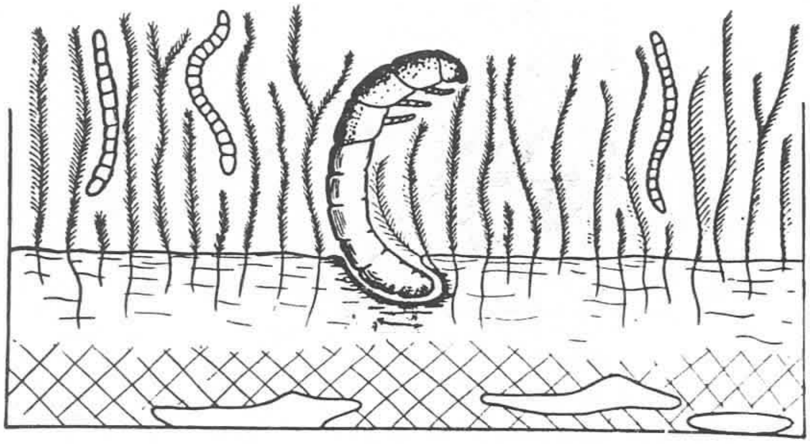


Fig. 6. The position of soil invertebrates in moss tundra during the wet and warm season (according to Stebayev)

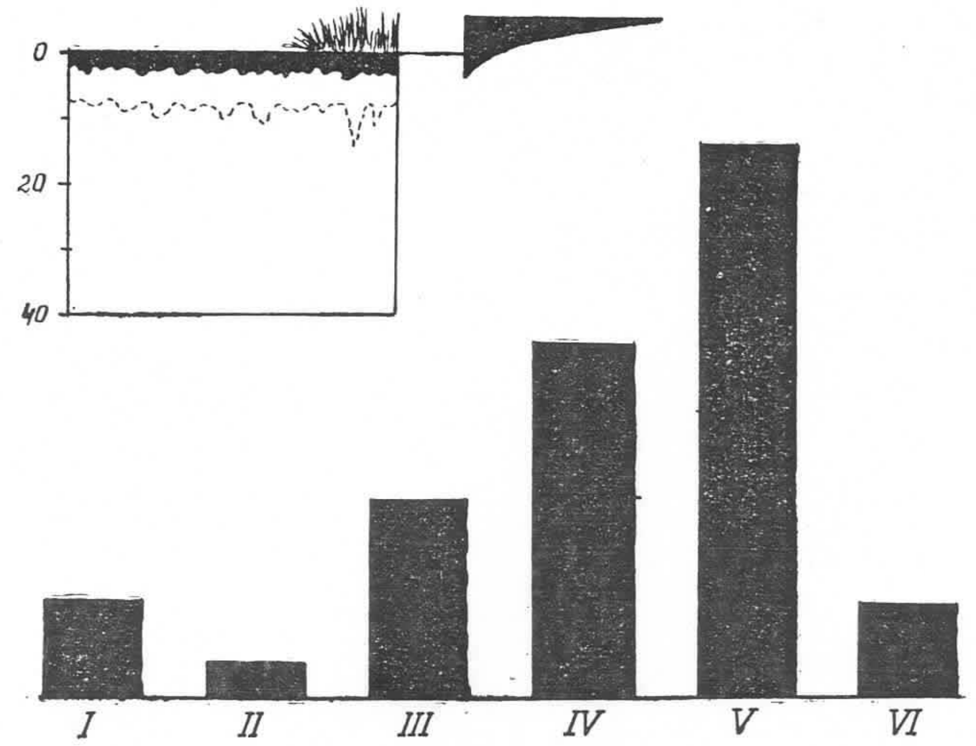


Fig. 7. Above: The character of the soil profile (right) and the mean distribution of larger invertebrates during the season of vegetation in tundra soil (left)
Below: Comparison of the mean population density of larger soil invertebrates under the typical natural plant canopy in different zonal soil types

I — Moss tundra soil. II — Podzolic soil of taiga. III — Dern-podzolic soil of southern taiga. IV — Grey forest soil of deciduous forest. V — Chernozem soil of steppes. VI — Sierozem soil of semi-desert

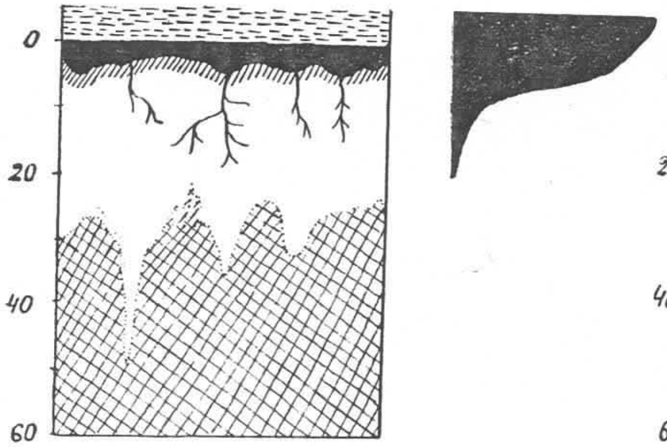


Fig. 8. Character of soil profile, and average distribution of invertebrates in different soil layers during the vegetation season in podzols of the taiga (coniferous forest)

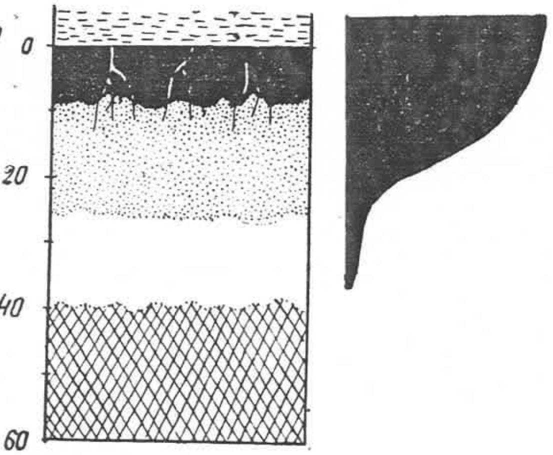


Fig. 9. The same, in dern-podzol soil of mixed forests

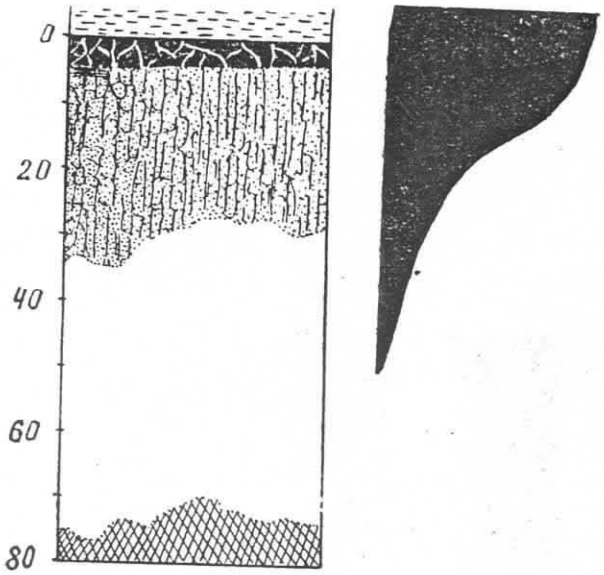


Fig. 10. The same, in grey forest soil of forest

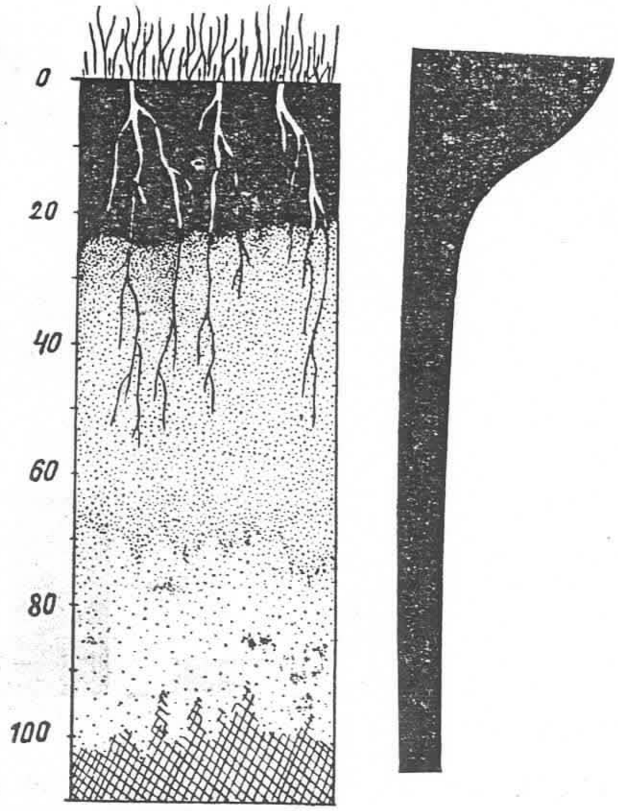
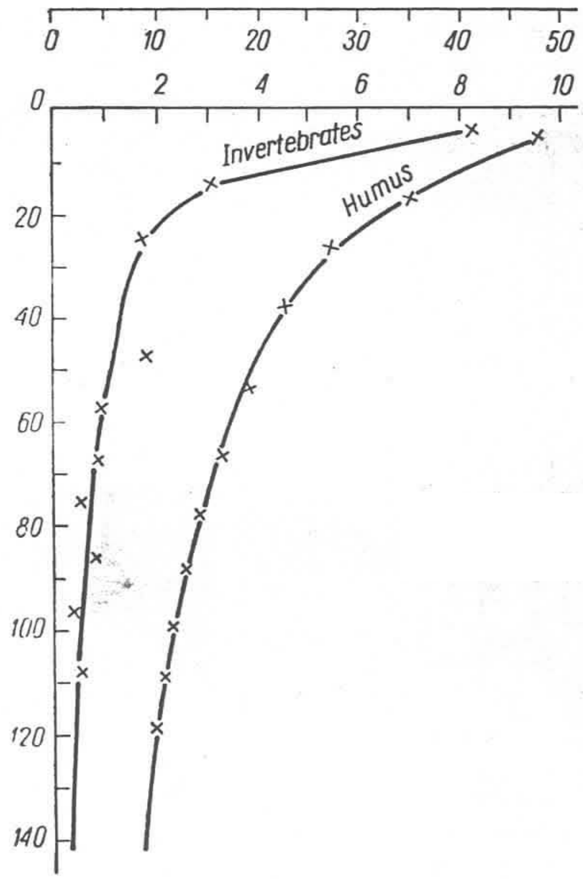


Fig. 11. The same, in chernozem of virgin steppe



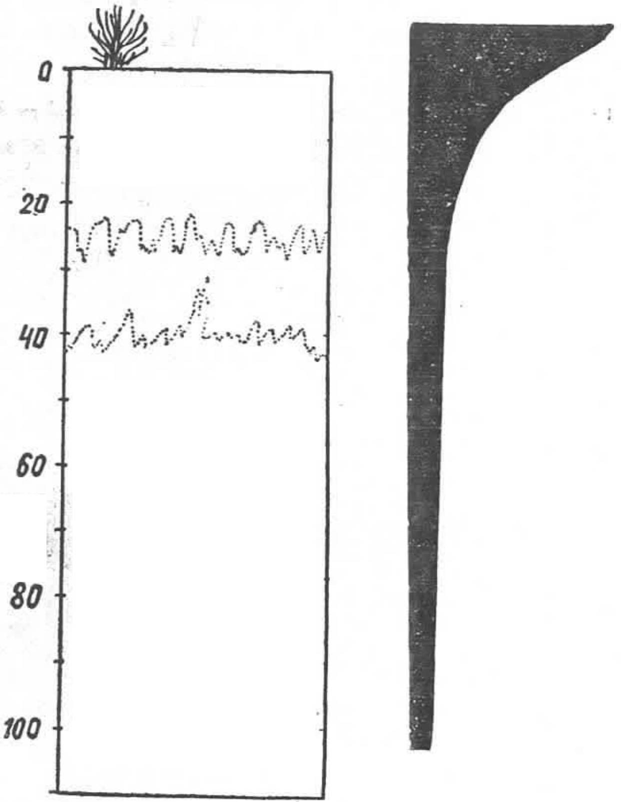


Fig. 12. Distribution of humus and average distribution of invertebrates during the warm period of the year in profile of chernozem soil

Fig. 13. Character of soil profile (left) and the average annual distribution of larger invertebrates in sierozem (desert grey) soil of semidesert (almost evenly distributed small content of humus in the soil layer)

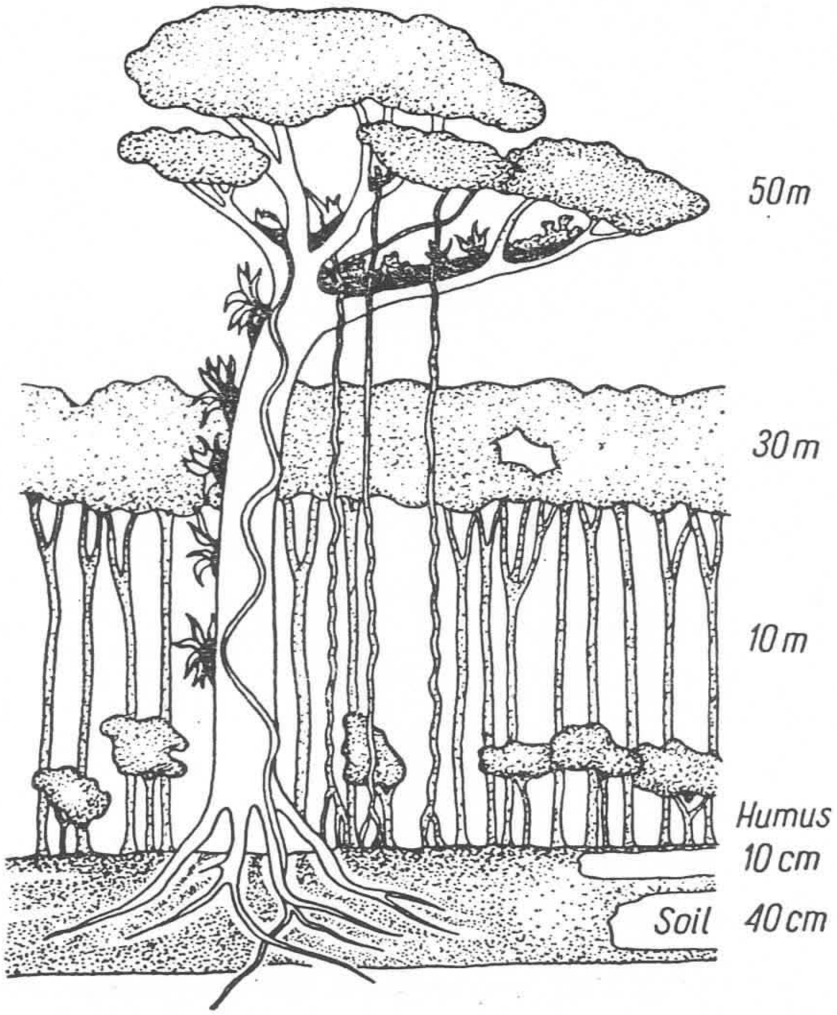


Fig. 14. Typical aspect of tropical rain forest plant cover (schematized after Delamare and Deboutteville 1951)

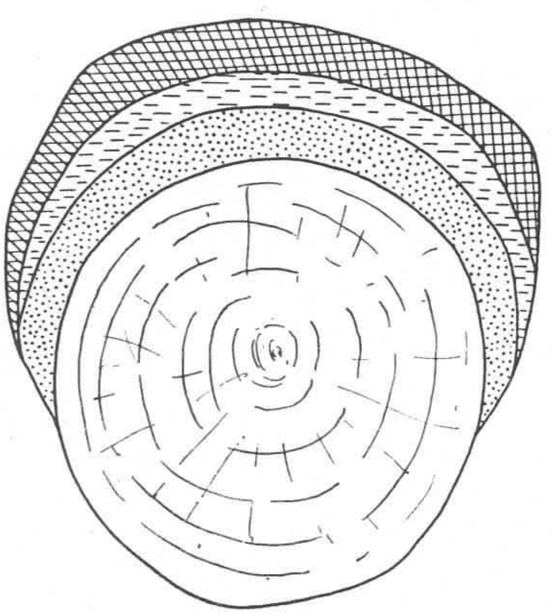


Fig. 15. The formation of differentiated soil layers on tree twig in the rain forest "soil suspendu" (according to Delamare and Deboutteville 1951)